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Continued reduction in population growth rate of grey seals at Sable Island

Diminution continue du taux de croissance de la population de phoques gris à l'île de Sable

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ABSTRACT

We conducted a digital-photographic aerial survey on Sable Island, Nova Scotia in January 2007 to estimate grey seal (*Halichoerus grypus)* pup production. A total of 48,036 pups was counted on the digital imagery. Given the high quality of the imagery, no correction for missed pups was necessary after analysis of ground-truthing plots. Correction for proportion of pups that died prior to the survey (0.0276) and the proportion of pups born before the survey (east colony 0.91, west colony 0.89), estimated total pup production was 54,500 with 95% confidence limits of 52,000 to 57,100 and standard error of 1,288. The 2007 estimate indicates that pup production on Sable Island has continued to increase, but that the rate of increase has declined over the past two successive surveys. Proportion of females giving birth at ages 4-7 yr, from the 1998-2002 cohorts, were significantly lower than those in the mid-late 1980s. The new estimate of pup production and new data on age of primiparity provide further indication of changes in vital rates of this population.

RÉSUMÉ

Nous avons réalisé un relevé aérien photo-numérique à l'île de Sable (Nouvelle Écosse) en janvier 2007, afin d'évaluer la production de jeunes phoques gris (*Halichoerus grypus*). Au total, l'imagerie numérique a permis de dénombrer 48 036 bébés phoques. Étant donné la grande qualité des images, aucune correction n'a été nécessaire pour tenir compte de bébés phoques manquants après analyse des parcelles vérifiées au sol. La correction visant à tenir compte de la proportion de nouveau-nés qui sont morts avant le relevé (0,0276) et de la proportion de ceux qui sont nés avant le relevé (colonie de l'est, 0,91, colonie de l'ouest, 0,89) a mené à une estimation totale de la production de nouveau-nés de 54 500, avec une limite de confiance de 95 % (52 000 à 57 100) et un écart type de 1 288. L'estimation de 2007 montre que la production de nouveau-nés dans l'île de Sable continue à augmenter, mais que le taux d'accroissement a diminué selon les deux derniers relevés. La proportion de femelles qui mettent bas entre 4 et 7 ans, issues des cohortes de 1998 – 2002, était considérablement inférieure à celle du milieu et de la fin des années 1980. La nouvelle estimation de production de bébés phoques et les nouvelles données sur l'âge des primipares est une indication supplémentaire de changements dans l'indice vital de cette population.

Introduction

One of the longest series of estimates of pup production comes from a study which began in 1962 at Sable Island, Nova Scotia. The number of grey seal (*Halichoerus grypus*) pups born at Sable Island has increased exponentially for the past four decades (Bowen et al. 2003). The grey seal is a generalist predator feeding on a wide range of demersal and small pelagic fishes (Bowen and Harrison 1994; Beck et al. 2007) in continental shelf ecosystems and inland seas on both sides of the North Atlantic Ocean. Within its Canadian range, the grey seal forages widely throughout the Scotian Shelf and the Gulf of St. Lawrence during the non-breeding season (Stobo et al. 1990; Bowen et al. 2007). Major grey seal breeding colonies are located on the sea ice in the southern Gulf of St. Lawrence and on Sable Island, Nova Scotia. Smaller colonies are found on near-shore islands off Cape Breton and along the Eastern Shore of Nova Scotia (Mansfield and Beck 1977; Hammill et al. 1998).

Here we report on the 2007 aerial photographic survey of grey seal pup production at Sable Island. Our objective was to test the hypothesis that the reduction in the rate of increase in grey seal production observed between 1997 and 2004 has persisted. Using long-term life history data from individually marked females, we also update trends in age of primiparity, a trait which is thought to be a relatively sensitive indicator of density-dependent changes in vital rates (Eberhardt 1977).

Methods

The estimation of pup production follows the approach given in Bowen et al. (1987), Myers and Bowen (1989) and Bowen et al. (2003, 2007). The number of pups born prior to the aerial survey is based on counts of live pups photographed. This number is then corrected for the fractions of live pups not detected on the imagery, pups that had died prior to the survey and hence were not visible on the imagery, and pups that were born after the survey was conducted.

The photographic census was conducted using a Piper Turbo Aztec "F" fixed-wing aircraft on 7 January between 11:12 and 14:19h (Atlantic Standard Time). The aircraft was equipped with a radar altimeter and motion compensation camera housing. Photographs (RGB 16 bit digital files) were taken with Vexcel Ultrcam D digital camera equipped with integrated in-flight GPS. This coupled with data from a differential GPS base station operating simultaneously on Sable Island during the survey permitted precise geo-referencing of each photograph. Twenty-four transects were flown at an altitude of ~350 m to provide complete photographic coverage of the island. Individual photographs had about 30% forward overlap and adjacent transects had 20% lateral overlap and a resolution of 3 cm.

Prior to reading the 1020 photographs, overlap of adjacent photographs was eliminated using geo-referencing software of Airbone Sensing to avoid double counting pups. Digital photographs were stored on a LaCie Drive and processed using a dual core 2.66 GHz desktop computer running the GIS software ERSI ArcMap 9.1. A grid layer was superimposed on each photograph and pups were virtually marked using a pup counting layer within the GIS.

Pup production estimates

Total pup production was estimated as follows:

$$N_{total} = \sum_{i=1}^{2} \left(\frac{count_i \bullet g}{(1-d) \bullet p_i} \right) \qquad (1)$$

where i = 1 and 2 for the east and west colonies, respectively, and *count* is the count of live pups on the positives, g is the correction for pups missed in the imagery, p is the estimated proportion born prior to the time of the survey in each stratum, and d is the estimated proportion of pups that had died up to the day of the photographic survey. Standard error of total pup production was calculated from the estimated variances of correction factors using the delta method for independent random variables (Goodman 1960, Mood et al 1974) as follows:

$$\text{var}\, N_i = N_i^2 \bullet \left(\frac{\text{var}\, p_i}{p_i^2} + \frac{\text{var}\, d}{d^2} \right)$$

where i = 1 and 2 for the east and west colony, respectively. Although pups were born over the entire island again in 2007, we retained the separate estimation for the west colony and the east colony because there was a clear break in the spatial distribution of pups near the Weather Station at the western end of the Island.

The proportion of live pups that were photographed but not detected on the positives (g) in Equation (1) was determined by comparing pups counted in the photographed ground plots to the number of pups counted by observers on the ground. The 10 rectangular ground plots were widely distributed throughout the east and west colonies. The corners of each plot were demarcated with red vinyl fabric (Fig. 1) enabling us to locate the plots on the colour digital photographs. The size of the plots varied so that each plot contained > 25 pups. Two researchers on the ground counted pups independently as close as possible to the time the survey aircraft was overhead. Differences between observers were resolved before going to the next plot.

Temporal distribution of births

Two kinds of information were used to model the temporal distribution of births over the course of the season: the duration of developmental stages of pups and temporal changes in the proportions of each developmental stage. Pups were classified into five developmental stages based on a combination of pelage colouration and body shape (Bowen et al. 2003). These stages were similar to those defined by Radford et al. (1978) and Kovacs and Lavigne (1986). To estimate the duration of each stage 52 pups were marked shortly after birth in 12 different areas (3-6 pups/area) on 16 December and the stage of each pup was recorded daily until the pup had reached the last stage. To estimate how the proportion in each developmental stage changed over time, we recorded pup stages over the course of the breeding season at nine widely distributed regions (different than the ground plots referred to above) on the island. Seven sites within each region were visited weekly following Bowen et al. (2003, 2007).

We estimated the temporal distribution of births using the method described in Bowen et al. (2007), based on the approach developed by Myers and Bowen (1989). We considered three distributions for the number of pups born over time (Table 1) and in all parameterizations, ρ is the scale parameter and κ is the shape parameter. We selected the model with the lowest Akaike's Information Criterion (AIC).

Pup mortality rate

To estimate the fraction of pups that may have died prior to the photographic survey, we regularly (~ every 3d) counted and marked the number of dead pups in another nine sites. These were well-defined areas of the colony selected because they were clearly demarcated such that the number of live pups photographed on the day of the survey could be determined.

Age of primiparity

Recently weaned (i.e., within ~ 2 weeks) grey seal pups were hot-iron branded with individual marks in 1985, 1986, 1987 and 1989 and again from 1998 through 2002. These branded females provided an opportunity to determine the age at first birth for individuals recruiting to the breeding population on the island. Females were judged to be primiparous if they had not previously been seen during a breeding season and were either observed pregnant or nursing the first breeding season they were sighted. Non-pregnant females are rarely seen among lactating females and fostering is also rare on Sable Island, so we can be reasonably confident that the first year a female was observed she was primiparous.

To determine if a branded female had returned to Sable Island during the breeding season, we conducted weekly censuses of the entire colony. Censuses were conducted by 4-8 researchers and the use of all terrain vehicles ensured that the colony was thoroughly searched. Typically, five or six censuses were conducted each year covering the entire season of births. Although some of the females branded on Sable Island as pups may give birth at other colonies, grey seals exhibit strong philopatry at other colonies, including Sable Island (W. Stobo unpublish data). Furthermore, Sable Island is by far the largest colony in the Northwest Atlantic and therefore we expected that most females would return to Sable Island to give birth for the first time. Although the number of females giving birth in Sable Island has increased dramatically, in 2007 there was still unoccupied habitat and other areas where the density of females was low such that there is no reason to expect that young females from the 1998 to 2002 cohorts would be excluded from the breeding colony. Statistical analyses were preformed using S-plus version 6.2 and SPSS version 11.5. The standard error (SE) is given as a measure of variability about means.

RESULTS

The aerial survey conducted on January 7 yielded a count of 48,036 pups, 25.0 % in the west colony and 75% in the east colony. Weather was optimal for the survey providing exceptionally quality imagery (Fig. 1).

The 10 ground-control plots contained from 36 to 81 pups (Table 1). In contrast to previous surveys, the imagery counts were equal to or greater than ground counts in 8 of the 10 plots. In the two plots were ground counts exceeded those from the imagery, the difference could be attributed to pups that were lying across one of the plot borders having moved outside of the plot by the time the photograph was taken. In no case were pups missed on the imagery. Therefore, no correction for missed pups was necessary.

Estimates of stage durations differed from those measured in 1997 with pups spending less time in stages 2 and 4 than they did in 1997 (Table 2). As stage classification is based on both the rate of pup fattening and coat colour, local environmental conditions and differences in maternal resource allocation presumably underlie these differences. However, the relative importance of these two factors remains to be investigated.

The developmental stage of 9,011 pups was recorded along ground transects in the nine regions widely distributed throughout the colony over a 37-day period from December 17 to January 22 (Appendix 1). Three models were fitted to estimate the distribution of births over time and from that the proportion of pups born by January 12 (Table 3). Date of the first birth was estimates as December 5 and December 10 for the east and west colonies, respectively, based on the oldest stage pups observed on our arrival on 15 December. These dates were used to define the limit of the left tail of the modelled distributions. All models fit reasonably well but, based on the AIC criteria, the Weibull model provided the best fit (Table 3).

The nine sites selected to estimate the proportion of pups that had died before the photographs were taken represented 5.3% of the live pups photographed. The mean proportion that had died was 0.0276 ± 0.0056 (Table 4).

Estimated N_{total} was 54,500 (rounded) with 95% confidence limits of 52,000 and 57,100 (based on log-normal distribution) and a SE of 1,288 (Table 5).

Bowen et al. (2007) showed that the number of females giving birth for the first time at age 4, 5 and 6 differed significantly among cohorts. Expressed as odds ratio, females were about 16 times more likely to give birth for the first time at age 4 during the mid to late 1980s than they were from 1998 to 2000. By contrast, females were more than twice as likely to give birth for the first time at age 6 yr compared to the mid to late 1980's cohorts. Additional data collected from the 1998 to 2002 cohorts confirm these conclusions (Table 6).

DISCUSSION

Pup production of grey seals at Sable Island increased exponentially at a rate near r_{max} for four decades (1962-1997; Bowen et al. 2003). Extrapolating the exponential model (Bowen et al. 2003) using the most accurate series of pup cohorts (i.e., 1976 to 1997) gave a predicted 2004 pup production significantly greater than that estimated (Fig. 2) suggesting that the rate of increase between 1997 and 2004 had declined (Bowen et al. 2007). Predicted pup production in 2007 from that exponential model is 88,000 compared to the estimated value of 54,500 providing further support for a decline in the rate of increase in this component of the grey seal population.

Sources of error in estimated pup production

Pup counts from the imagery must be corrected for several factors to estimate total pup production. First, as found in previous surveys, some live-pups may be missed on the photographs resulting in an underestimate. However, the high quality of the digital images in the present survey made this correction unnecessary. Second, pups that died before the aerial survey was conducted will not have been counted. On Sable Island, drifting sand and snow soon cover dead pups making them invisible on the positives. We corrected for pup mortality and so this should not be a source of bias. We also estimated pup stage durations used to fit the temporal distribution of births model. Model fits to these data were good and thus this should not be a source of error.

Trend in pup production

Bowen et al. (2007) noted that a decrease in the rate of increase of pup production on Sable Island could have been caused by density-dependent changes in vital rates or that 2003 could have been a poor year (perhaps low food abundance) such that fewer females gave birth in 2004 resulting in a lower estimate than expected. However, the results from the current aerial survey indicate that the reduction the rate of increase in pup production has continued providing further support for the hypothesis that density-dependence may be limiting the rate of increase.

Pinnipeds have several characteristics that argue for extrinsic rather than intrinsic population regulation (Wolff 1997). Two density-dependent factors which may limit the population are food and space for parturition and pup rearing. Given that unused habitat is still available on Sable Island and along the coast of eastern Canada and northeastern United States, food is more likely to regulate grey seal numbers, consistent with the general view that most large mammals are regulated by food supply (Sinclair 1996). This was suggested by the marked decrease in odds of being primiparous at age 4 yr in recent cohorts compared to those in the 1980s (Bowen et al. 2007) and is further supported by the addition data on the proportion recruited at age of recent cohorts compared to those in the mid to late 1980s.

There are now two consecutive estimates of pup production indicating the exponential growth model is no longer an appropriate description of dynamics. With these estimates and the recent life history data showing a change in the odds of giving birth for the first time at age 4 yr over five successive cohorts, the case for density-dependent changes is becoming more compelling.

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Table 1. Number of grey seal pups counted on 10 ground plots and from digital imagery of those plots on 7 January, 2007.

	Number of pups counted			
Location	Ground	Imagery	Difference	Difference (%)
BIO	36	36	0	0.00
EL Dune	52	54	-2	-3.70
NB Steeple flats	50	50	0	0.00
Blowout South Beach	81	86	-5	-5.81
CWS west	59	63	-4	-6.35
CWS east	45	48	-3	-6.25
Lakeshore	43	43	0	0.00
SB Steeple Flats	45	42	3	7.14
Washover SB	45	45	0	0.00
Washover west	74	72	2	2.78

Table 2. Estimates of stage durations from daily records of 52 pups followed from birth to the last stage in 2007 and comparable data from 1997. Durations fitted with a gamma distribution.

	2007				1997			
Stage	Common Shape	Rate	Mean (d)	Variance	Common Shape	Rate	Mean (d)	Variance
1	24.51	8.31	3.0	0.35	21.22	5.46	3.3	0.81
2	24.51	7.98	3.1	0.39	21.22	5.25	4.6	1.21
3	24.51	2.06	11.9	5.76	21.22	2.02	11.0	7.84
4	24.51	4.63	5.3	1.14	21.22	3.01	7.6	3.92

Table 3. Estimates of the proportion of pups born by January 7, 2007 based on three model fits for east and west colony. Standard error given in parentheses.

Colony	Model	Shape (se)	Rate(se)	Proportion born (se)	AIC
East	Log-logistic	2.32 (0.17)	0.046 (0.0035)	0.724 (0.046)	12511.52
	Gamma	2.84 (0.31)	0.128 (0.021)	0.819 (0.040)	12502.96
	Weibull	2.13 (0.10)	21.86 (0.87)	0.910 (0.022)	12456.22
West	Log-logistic	3.01 (0.34)	0.043 (0.002)	0.744 (0.050)	9178.34
	Gamma	4.06 (0.78)	0.169 (0.041)	0.800 (0.045)	9201.4
	Weibull	2.68 (0.167)	24.27 (0.59)	0.897 (0.021)	9084.78

Distribution	Density Function	Number of Parameters
Gamma	$\rho(\rho t)^{\kappa-1}\exp(-\rho t)$	2
Weibull	$\kappa\rho(\rho t)^{\kappa-1}\exp[-(\rho t)^{\kappa}]$	2
Log-Logistic	$\kappa\rho^{\kappa}t^{\kappa-1}[1+(t\rho)^{\kappa}]^{-2}$	2

ρ=scale, κ=shape parameter

Table 4. Estimates of the proportion of pups that died up to 6 January, 2007 at 9 sites on Sable Island.

Area	Dead	Total alive	Proportion dead
Beck's Cove	9	152	0.059
Blowout	8	386	0.021
CWS	16	347	0.046
EL cut North Beach	2	219	0.009
EL dune, North Beach	6	428	0.014
LX West. North Beach	4	162	0.025
North Beach, West Boathouse	6	159	0.038
No.4 West	11	455	0.024
7.8 Cove	3	250	0.012

Table 5. Estimate of grey seal pup production on Sable Island in 2004 with SE in parentheses.

	West colony	East colony	Sable total
Pup counts from positives	12,018	36,018	48,036
Proportion born 7th	0.897(0.021)	0.910 (0.022)	
Dead pup correction	0.0276 (0.0056)	0.0276 (0.0056)	
N_{total}	13,778	40,704	54,500[1]
95% Confidence limits	13,000-14,600[1]	39,000-42,500[1]	52,000-57,100[1]

[1] rounded to the nearest hundred

Table 6. Number (n) and percentage (of total) of grey seal females giving birth at ages 4 - 7 yr from cohorts branded in 1985 through 2002.

							Recruited (%)			
Cohort	4	5	6	7	Total	n	Age 4	Age 5	Age 6	Age 7
1985	25	98	49	30	202	400	6.3	30.8	43.0	50.5
1986	63	81	45	18	207	400	15.7	36.0	47.3	51.8
1987	42	70	53	37	203	400	10.5	28.3	41.5	50.8
1989	34	93	27	85	239	500	6.8	25.4	30.8	47.8
							9.8	**30.1**	**40.6**	**50.2**
1998	0	17	14	13	44	150	0.0	11.3	20.7	29.3
1999	0	40	35	15	90	250	0.0	16.0	30.0	36.0
2000	3	25	19	13	60	250	1.2	11.2	18.8	24.0
2001	3	24	17		44	250	1.2	10.8	17.6	
2002	6	16			22	250	2.4	8.8		
							2.9	**11.6**	**21.8**	**29.8**
Total	176	464	259	211	1111					

Fig. 1. Example of digital photograph from the 2007 survey showing pups identified (black dots).

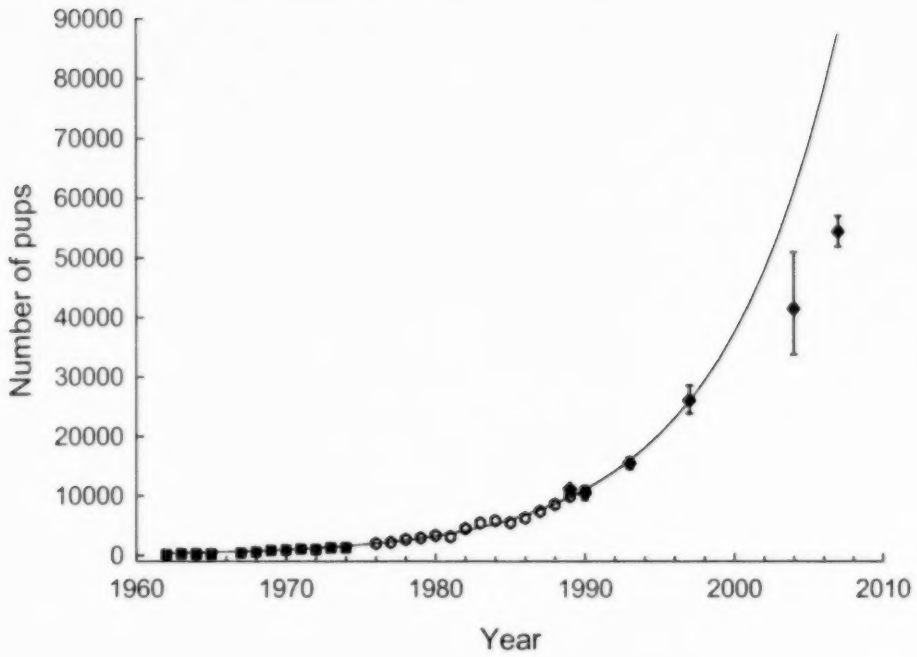

Fig. 2 Trend in grey seal pup production on Sable Island, 1962 to 2007, based on incomplete tagging (1962-1974), complete cohort tagging (1976-1990) and aerial photographic surveys (1989-2007). Error bars are approximate 95% confidence limits. Solid line represents an exponential curve fit to the 1976 to 1997 estimates.

Appendix 1. Stage composition of grey seal pups during the 17 December 2006 and 22 January 2007 breeding season on Sable Island.

Date	12/17/2006

Sum of Count	Stage					
Location	1	2	3	4	5	Grand Total
1	35	64	21	0	0	120
2	45	57	4	0	0	106
3	56	46	4	0	0	106
4	45	68	6	0	0	119
5	37	61	9	0	0	107
6	29	65	6	0	0	100
7	55	48	0	0	0	103
8	68	38	0	0	0	106
9	55	48	0	0	0	103
11	55	53	0	0	0	108
Grand Total	480	548	50	0	0	1078

Date	12/18/2006

Sum of Count	Stage					
Location	1	2	3	4	5	Grand Total
10	81	41	0	0	0	122
12	81	25	0	0	0	106
Grand Total	162	66	0	0	0	228

Date	12/26/2006

Sum of Count	Stage					
Location	1	2	3	4	5	Grand Total
13	39	40	58	0	0	137
14	33	42	52	0	0	127
15	31	49	55	0	0	135
16	23	45	52	2	0	122
17	28	61	54	2	0	145
18	39	40	58	0	0	137
19	33	54	43	1	0	131
20	36	52	39	1	0	128
21	23	63	34	1	0	121
Grand Total	285	446	445	7	0	1183

Date	12/27/2006

Sum of Count	Stage					
Location	1	2	3	4	5	Grand Total
22	36	52	44	0	0	132
23	26	54	50	0	0	130
24	19	60	54	0	0	133
Grand Total	81	166	148	0	0	395

Date	1/1/2007

Sum of Count	Stage					
Location	1	2	3	4	5	Grand Total
25	14	32	75	1	0	122
26	13	43	71	4	0	131
27	9	37	83	7	1	137
28	13	32	73	13	0	131
29	17	48	57	0	0	122
30	11	50	60	6	0	127
31	23	69	9	1	0	102
32	3	52	48	3	0	106
33	18	78	106	1	0	203
34	17	95	104	0	0	216
35	31	119	60	0	0	210
36	28	79	112	6	0	225
Grand Total	197	734	858	42	1	1832

Date	1/8/2007

Sum of Count	Stage					
Location	1	2	3	4	5	Grand Total
37	0	36	42	29	14	121
38	5	52	44	13	3	117
39	0	40	46	15	6	107
40	0	39	53	13	5	110
41	5	16	54	44	24	143
42	7	29	66	30	15	147
43	7	26	70	36	14	153
44	7	25	76	25	13	146
45	22	40	101	14	2	179
46	4	30	98	33	4	169
47	16	42	82	19	7	166
48	9	57	109	9	1	185

Grand Total	82	432	841	280	108	1743

Date	1/15/2007

Sum of Count	Stage					
Location	1	2	3	4	5	Grand Total
49	1	12	43	29	34	119
50	0	15	24	24	68	131
51	4	19	65	24	29	141
52	1	5	28	37	66	137
53	0	12	53	33	32	130
54	1	11	40	40	58	150
55	1	16	61	46	43	167
56	6	15	86	44	15	166
57	2	13	85	46	43	189
58	4	9	90	58	29	190
59	9	23	95	46	43	216
60	4	21	97	50	32	204
Grand Total	33	171	767	477	492	1940

Date	1/22/2007

Sum of Count	Stage					
Location	1	2	3	4	5	Grand Total
61	0	5	53	43	39	140
62	0	2	35	48	53	138
63	0	4	60	64	60	188
64	2	5	48	41	50	146
Grand Total	2	16	196	196	202	612